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Composition patterns of ornamental flora in the Czech Republic

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Abstract

Ornamental plants are an important component of urban floras and a significant source of alien plant invasions to the surrounding landscapes. We studied ornamental flora across 174 settlements in the Czech Republic, Central Europe. The aims of the study were to (i) identify clusters of sites that are defined as distinctive groups of ornamental taxa reflecting environmental or socioeconomic factors and (ii) apply the classification approach which is traditionally used for spontaneous vegetation in order to evaluate the potential of different settlement types to act as source sites of invasive species. The inventories were classified in a similar manner that is generally applied to spontaneous vegetation using the COCKTAIL method. Diagnostic taxa were classified in a repeatable manner into 17 species groups, forming five distinctive clusters with ~70% of sites attributed to one cluster. The species pools of the clusters differed in their representation of species with native or alien status and different life forms. The following clusters were distinguished, based on the prevailing type of settlement: (1) old villas neighbourhoods of towns, (2) upland settlements, (3) modern neighbourhoods, (4) old rustic settlements and (5) modern rustic settlements. Similar to spontaneous vegetation, the classification of ornamental flora reflects both basic natural gradients (i.e. altitude) and man-made factors (i.e. the preferences for certain plants and associated management practices). Alien taxa associated with modern neighbourhoods are characterised by a relatively higher invasion potential than those from, for example, old rustic settlements. This is especially true for woody species which can spread in ruderal habitats as a result of urban sprawl. Our results showed that the classification method, commonly used to analyse vegetation data, can also be applied to ornamental flora.

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Keywords
homegardens, invasion potential, urban, vegetation classification

Introduction

The recent increase in the knowledge of alien floras in countries worldwide (e.g. Pyšek et al. 2012, 2017; van Kleunen et al. 2015), as well as in the theory of biological invasions (e.g. Catford et al. 2009; Blackburn et al. 2011; Kueffer et al. 2013; Enders et al. 2019) has drawn the attention of researchers, amongst other topics, towards the ecological consequences of ornamental introductions (e.g. Thompson et al. 2003; Gaston et al. 2005, 2007; Smith et al. 2006; Loram et al. 2008a; van Heezik et al. 2013; Hulme et al. 2018; van Kleunen et al. 2018). Several studies integrate ecological data with socioeconomic aspects in ethnobotanical research, addressing the utilisation of plants by traditional societies (Vogl et al. 2004; Loram et al. 2008b; Davoren et al. 2016; Palliwoda et al. 2017), people's plants preferences (Kendal et al. 2012b) or with landscape design (Groening and Wolschke-Bulmahn 1989; Redman et al. 2004). However, the acquisition, cultivation, escape and formation of invading populations of ornamental aliens is a gradual process that is rarely studied in its entirety (but see Kowarik 2005; Daehler 2008; Cook et al. 2012; Kowarik and Pyšek 2012; Mayer et al. 2017; van Kleunen et al. 2018).

Ornamental plants represent an important component in the urban space (Chocholoušková and Pyšek 2003; Kowarik 2005; Botham et al. 2009; Pyšek and Chytrý 2014; Pergl et al. 2016b), as well as a significant source of invasive species as a result of escapes from private or public gardens (Reichard and White 2001; Dehnen-Schmutz et al. 2007; Hanspach et al. 2008; Hulme 2011; Pyšek et al. 2011; Gregor et al. 2012). Many taxa initially escape and spread in spatially restricted areas in the surroundings of gardens and then spread and colonise more distant vegetation. Such naturalisation foci may appear as a result of the combined effects of local popularity of a given taxon, regardless of its invasion status (Humair et al. 2014), suitable natural and cultural conditions (Marco et al. 2010), abundant propagation in cultivation and easy semi-spontaneous establishment in gardens. For example, many ornamental taxa become naturalised or even invasive in peri-urban belts or along motorways (Yang et al. 2015). This implies that (i) most naturalised ornamentals come from populations that are already pre-adapted to the local conditions (Mack 2000; Pyšek et al. 2011), (ii) the naturalised taxa are not distributed evenly across various natural and cultural gradients, but they are concentrated in specific conditions which are generally favourable for many escaping taxa and (iii) where there is a suitable set of introduction pathways and dispersal vectors (von der Lippe and Kowarik 2007; Wilson et al. 2009).

The horticulture industry is a major pathway for introductions of alien plants worldwide (Hulme et al. 2018; van Kleunen et al. 2018). It was shown that species introduced intentionally are more likely to have negative impact than those introduced unintentionally (Pergl et al. 2017) – many naturalised ornamentals have negative impacts on

native biodiversity (Vilà et al. 2010; Pyšek et al. 2012) or hybridise with native species (Klonner et al. 2017). However, it has also been shown that alien species introduced unintentionally can be successfull invaders and also have high impact (Pyšek et al. 2011; Rumlerová et al. 2016). These factors may become significant in the era of changing climate (Klonner et al. 2017; Haeuser et al. 2018). Although the majority of alien species, grown as garden ornamentals, can only survive when planted under intensive management, a considerable number escape without human assistance and establish outside gardens (Pergl et al. 2016a; Dullinger et al. 2017; Mayer et al. 2017). In a previous study, we recorded 1,834 ornamental taxa in cultivated areas of 174 settlements in the Czech Republic, central Europe, of which 23% are known to escape from the cultivation (Pergl et al. 2016b). In the alien flora of the Czech Republic, 56% of the taxa have been recruited from escaping ornamental plants (Pyšek et al. 2012). Similarly, amongst 78 species cited in the Black List of alien species in the Czech Republic (i.e. national list of noxious weeds and pests), 51 species are planted as ornamentals and this includes some of the most invasive species such as *Heracleum mantegazzianum* or *Reynoutria* (syn. *Fallopia*) spp. (Pergl et al. 2016a). Detailed information on the origin, behaviour and secondary spread of the species at a site and in its neighbourhood can be obtained by questioning the local growers and horticulturalists and this knowledge can be useful in assessing the future risks of invasions (Kowarik 2005; Dehnen-Schmutz and Conroy 2018).

As shown by Lososová et al. (2012) and Štajerová et al. (2017), the composition of urban floras is determined by the availability of habitats and their spatial distribution, as well as by climate. Similarly, habitat heterogeneity influences the composition of ornamental flora in settlements. Moreover, the composition of ornamental flora reflects natural gradients in environmental conditions as well as the complex interplay of cultural and socioeconomic factors (e.g. Sukopp 2002; Loram et al. 2008a, b; Kendal et al. 2012a; Cubino et al. 2014, 2016; Lowenstein and Minor 2016). Reasons for planting are various and often remain hidden. Garden flora is dominated by rare and transient species that are surviving due to human care and are weakened by interspecific competition (Pergl et al. 2016b). The trade-off in research approaches between small-scale surveys of individual gardens covering restricted regions (e.g. Thompson et al. 2003) on one side and large scale studies on the other (e.g. Pergl et al. 2016a), shows that at the scale of individual gardens, some species appear to be rare (they occur at low abundances), but their local frequencies are rather high. Previous studies suggest that sampling whole settlements compared to inventories of individual gardens overestimates the proportion of rare species in the total flora, but this can be sufficiently compensated when accounting for the measures of abundance (Thompson et al. 2003; Smith et al. 2006; Acar et al. 2007; Pergl et al. 2016b).

Bearing this complexity in mind, we tested whether some repetitive ornamental species assemblages occur in human settlements. The main aim of the study is to identify clusters of sites that are defined as distinctive groups of ornamental taxa reflecting environmental or socioeconomic diversity by applying a modern vegetation classification approach and to assess the composition of ornamental flora at different settlement types in relation to aliens, therefore acting as source sites for the invasive species.

Methods

Study sites and recorded data

We used our previous research data on the ornamental flora in the Czech Republic (Pergl et al. 2016b). The ornamental flora was recorded at 174 urban localities (further referred to as 'sites') covering the main gradients of environmental (see Chytrý 2012) and socioeconomic conditions on the urban-rural gradient. Our study included records from ~ 3% of municipalities in the Czech Republic. The site sampling contained villages, towns, cities, garden allotments, cemeteries, areas of dispersed farmhouse settlement and new suburban residential areas. For relatively small villages of up to ~2000 inhabitants, the village was considered as a single site, whereas in towns and cities, several sites of similar urban character were included in this study. At each site, the ornamental flora was recorded in private gardens, as well as in public areas, with at least five gardens per site studied in detail. Sampling was based on the ability to enter private gardens and other gardens were surveyed from behind the fence (see Pergl et al. 2016b). Data were collected between June and August 2011–2013 by 11 botanists, most of them having met before fieldwork to adjust the methodology. At each site, we recorded both alien and native plants cultivated as ornamentals in private gardens and public spaces, except for spring geophytes and conifers that were excluded because this involved repeated visits to the sites to record both spring and summer aspects. To reduce the potential bias in sampling effort and different taxonomic expertise of involved botanists, an approach of aggregated taxa for complex taxon groups was used and the rarely recorded species were excluded from the analysis (see below). For each taxon at each site, the local population size (hereafter referred to as 'abundance') was estimated by using an ordinal scale, ranging from species present in a single garden (i.e. low abundance), species present in more than one garden but less than 30% of gardens (i.e. medium abundance), to commonly occurring taxa, recorded in more than 30% of gardens (i.e. high abundance). The final taxon × site matrix consisted of 35,725 records for 1,514 aggregated taxa (after taxonomic standardisation; see Pergl et al. 2016b, Supl. material 1 for a detailed description and data and Fig. 1 for data distribution).

Alien status was assigned to each taxon based on Pyšek et al. (2012). Definition of invasion status follows Richardson et al. (2000) and Blackburn et al. (2011). Persistence was classified as persistent (i.e. core) or transient part of the flora (MacArthur 1960; Magurran and Henderson 2003; Coyle et al. 2013). The categorisation is explained in detail in Pergl et al. (2016b) and was based on the taxon status, cultivation requirements and abundance. Data on species naturalisation status and abundance were taken from Pyšek et al. (2012). Native taxa (taxonomy taken from Danihelka et al. 2012) and all naturalised alien taxa with high abundance or scattered casual aliens were classified as core taxa. Frost-sensitive cultivated plants and casual aliens that vanished or were known from a single occurrence were classified as transient (see Supl. material 1 for further details on the sampling methods). If the aggregated taxon contained an alien taxon, then it was considered as alien in the analysis.

Classification of sites using the COCKTAIL method

We examined the compositional variation of ornamental flora in sites using the supervised classification of the COCKTAIL method (Bruelheide 2000). The method is based on statistical measures of fidelity (i.e. the species concentration in a classification unit). Further, observed species frequencies within a classification unit (i.e. site) are compared with the frequencies expected under random distribution and this controlled procedure creates groups of species (Chytrý et al. 2002). The supervised classification is partially influenced by the observer by setting initial conditions of analysis (i.e. initial species with the highest fidelity values entering the process, see details below). The COCKTAIL method uses presence/absence data and is therefore appropriate for datasets with varying species abundances.

As a fidelity measure, we used the *phi* coefficient (Chytrý et al. 2002) that range from –1 to 1. The *phi* value of 1 is for taxa occurring in all sites of a cluster and are absent elsewhere. The *phi* coefficient of association describes the correlation between two categorical factors in a 2 × 2 contingency table (Sokal and Rohlf 1995). A positive value of *phi* means that there is a positive correlation between a species and an existing species group. An advantage of the *phi* coefficient is its independence from the size of data; however, it depends on the relative cluster size. Therefore, we standardised the *phi* values to equate to the cluster size, according to Tichý and Chytrý (2006). Only taxa with both significant concentration in particular clusters (using Fisher's exact test and the significance level of $p < 0.01$) and a *phi* coefficient of ≥ 0.30 were considered as *diagnostic*. Fisher's test excludes some rare taxa that could become diagnostic by chance and is considered as a correction for the calculation of statistical significance for fidelity measures. The threshold value was selected subjectively in order to obtain a reasonable number of diagnostic species and is also comparable to other studies (see for example, Jarolímek and Šibík 2008 or Chytrý 2009). See Table 1 for the composition of assemblages and selected diagnostic taxa in all clusters.

First, we started the clustering algorithm with initial diagnostic species. In most cases, however, the same species group is obtained irrespective of which species of the group is chosen to start the algorithm (Bruelheide 1995). Second, further species were added to the species group if their association to one or more species in the group exceeded a certain fidelity threshold (see above for details). The expected and observed cumulative distribution functions for sites were calculated using interspecific association between the selected species and other species in the dataset. Only groups that formed three or more sites were used for further analyses. We used the logical operator "AND" in our COCKTAIL definitions of classification units, when linking the plant assemblages in the JUICE 7.0 programme using a standardised process (Tichý 2002). Details on the COCKTAIL algorithm, defining the species groups, interspecific associations and group aggregation are described step by step at http://www.sci.muni.cz/botany/juice/mang.htm.

To describe gradients in environmental, social and economic traits, we used data from the Czech Statistical Office (www.cuzk.cz) and the Czech Hydrometeorological Institute (www.chmi.cz) shown in Table 2. The list of characteristics for individual sites with architectonical structure, socioeconomic and environmental factors can be found in Suppl. material 2.

Table 1. Lists of diagnostic taxa composed of 17 COCKTAIL species groups (i.e. five clusters). The numbers of sites selected by a species group are presented in brackets. Planted species (in bold), casual aliens (*), naturalised incl. invasive aliens (#).

Cluster	Diagnostic taxa
1 – Old villas neighbourhoods of towns	
Asarum europaeum group (53): *Asarum europaeum*; *Hepatica nobilis*; *Impatiens balsamina* *Pseudofumaria lutea* group (85): *Asarum europaeum*; *Dryas octopetala*; *Lysimachia nummularia*; *Pseudofumaria lutea* *Rhododendron* group (170): *Ligustrum vulgare*; *Rhododendron* spp., *Yucca filamentosa*	***Acaena* spp.**, *Antennaria dioica*, *Aquilegia flabellata**, *Asarum europaeum*, *Asplenium trichomanes*, ***Athyrium nipponicum***, *Carex muricata* agg., *Cymbalaria muralis**, ***Daphne arbuscula***, *Datura stramonium**, ***Erica cinerea***, ***Euphorbia milii***, ***E. pulcherrima***, *Hacquetia epipactis*, ***Heuchera sanguinea***, *Impatiens balsamina**, *Lilium martagon*, *Lysimachia nummularia*, *Matteuccia struthiopteris#*, *Parnassia palustris*, *Phyllitis scolopendrium*, *Robinia pseudacacia#*, *Rosa ×centifolia** et *R. damascena**, *Sarracenia* sp.* et hybr., *Sedum hispanicum#*, *Verbascum thapsus*
2 – Upland settlements	
Salix euxina group (28): *Glebionis segetum*; *Papaver croceum*; *Salix euxina* *Aubrieta* group (134): *Aubrieta deltoidea*; *Gentiana acaulis* et *G. clusii*, *Saxifraga* sect. *Euaizoonia* *Athyrium filix-femina* group (113): *Athyrium filix-femina*; *Helianthus ×laetiflorus*; *Sedum anacampseros*	*Achillea ptarmica*, *Allium senescens*, ***Arisaema* spp.**, ***Artemisia abrotanum***, ***Begonia* aff. *×tuberhybrida***, *Callistephus chinensis**, *Carex elata*, *Cymbalaria pallida**, *Dianthus barbatus#*, *Digitalis purpurea#*, *Dryopteris carthusiana*, ***Geranium ibericum* et *G. platypetalum* et *G. ×magnificum***, *Glebionis segetum**, ***Hebe* small-leaved spp. et hybr.**, *Helianthus ×laetiflorus#*, ***Heuchera cylindrica***, *Hordeum jubatum#*, *Iris pseudacorus*, *Jovibarba globifera*, ***Kalanchoe blossfeldiana***, *Lilium bulbiferum*, ***Magnolia kobus***, ***Mauranthemum paludosum***, *Miscanthus floridulus** et *M. ×giganteus**, *Oxalis corniculata#*, *Papaver croceum**, ***Plectranthus forsteri***, ***Primula denticulata***, *Pseudolysimachion spicatum*, *Salix euxina*, ***Sedum anacampseros***, *S. forsterianum**, *Sempervivum* sp.* et hybr., *Staphylea pinnata*, *Symphyotrichum dumosum**, *S. novae-angliae**, *Tradescantia ×andersoniana**
3 – Modern neighbourhoods	
Acer palmata group (131): *Acer* sect. *Palmata*; *Campsis grandiflora*; *C. radicans* et *C. ×tagliabuana*; *Magnolia* aff. *×soulangeana*; *Salix matsudana* cv. *Tortuosa* et *S. ×sepulcralis* cv. *Erythroflexuosa* *Pennisetum alopecuroides* group (118): *Hydrangea arborescens*; *Pennisetum alopecuroides*; *Pyracantha coccinea* *Perovskia* spp. group (71): *Perovskia abrotanoides* et *P. atriplicifolia*; *Caryopteris ×clandonensis*; *Jasminum nudiflorum*, *Santolina chamaecyparissus*	*Acer platanoides*, ***A.* sect. *Palmata***, *Ailanthus altissima#*, ***Aristolochia macrophylla***, ***Asparagus densiflorus***, **Bambusoideae tall small-leaved taxa**, ***Campsis grandiflora* et *C. radicans* et *C. ×tagliabuana***, ***Caryopteris ×clandonensis***, *Catalpa bignonioides**, ***Cortaderia selloana***, ***Hamamelis* spp.**, ***Heuchera* aff. *americana***, ***Hydrangea serrata***, ***Jasminum nudiflorum***, *Koelreuteria paniculata**, *Laburnum anagyroides#* et *L. ×watereri#*, *Lathyrus vernus*, ***Lonicera* aff. *sempervirens***, ***Magnolia* aff. *×soulangiana***, *Nepeta racemosa** et *M. ×faassenii**, *Pennisetum alopecuroides**, ***Perovskia abrotanoides* et *P. atriplicifolia***, *Populus nigra*, *Prunus cerasifera#* et *P. ×cistena#*, *Pyracantha coccinea#*, *Santolina chamaecyparissus**, ***Silene uniflora***, ***Spiraea* aff. *×cinerea***, ***Syringa ×prestoniae***, ***Tradescantia pallida***, *Ulmus* aff. *minor*, *Viburnum rhytidophyllum** et *V. ×pragense**, ***V. tinus***
4 – Old rustic settlements	
Calendula officinalis group (162): *Calendula officinalis*; *Callistephus chinensis*; *Echinacea purpurea*; *Tagetes erecta* *Mahonia aquifolium* group (166): *Alcea rosea*; *Antirrhinum majus*; *Asparagus officinalis*; *Campanula persicifolia*; *Mahonia aquifolium* *Agrimonia* aff. *eupatoria* group (84): *Agrimonia* aff. *eupatoria*; *Allium schoenoprasum*; *Anethum graveolens*; *Levisticum officinale*; *Rheum rhabarbarum*, *Vaccinium corymbosum* *Nigella damascena* group (67): *Nigella damascena*; *Lavatera trimestris*; *Limonium sinuatum*	*Aconitum* aff. *napellus*, *Agrimonia* aff. *eupatoria*, *Anethum graveolens**, ***Asclepias tuberosa***, *Bassia scoparia#*, ***Cleome hassleriana***, ***Coreopsis basalis***, ***C. rosea***, *Cosmos bipinnatus**, ***C. sulphureus***, ***Cyclamen persicum***, ***Dracaena* sp.**, ***Eupatorium purpureum***, ***Iris ensata***, ***Leucanthemopsis alpina***, *Levisticum officinale**, ***Ligularia stenocephala***, ***Limonium sinuatum***, ***Lonicera fragrantissima* et *L. ×purpusii***, *Malope trifida**, *Malus* spp.*, *Mentha longifolia*, *Mentha ×verticillata*, ***Mimulus aurantiacus***, ***Myrtus communis***, *Nigella damascena**, ***Pentas lanceolata***, *Polemonium caeruleum*, ***Primula japonica***, ***Rhodanthe chlorocephala***, ***Sidalcea malviflora***, ***Silene banksia***, ***Skimmia japonica***, ***Syringa ×chinensis***, *Thladiantha dubia**, *Vaccinium corymbosum**, ***Veronica virginica***, ***Viburnum farreri* et *V. ×bodnatense***
5 – Modern rustic settlements	
Rudbeckia laciniata group (144): *Cosmos bipinnatus*; *Delphinium ×cultorum*; *Heliopsis helianthoides*; *Rudbeckia laciniata*; *Salvia officinalis* *Commelina communis* group (81): *Portulaca grandiflora* et hybr.; *Euphorbia marginata*; *Commelina communis* *Anemone sylvestris* group (87): *Anemone sylvestris*; *Festuca gautieri*; *Pseudolysimachion incanum*; *Veronica austriaca* et *V. caespitosa* *Centaurea dealbata* group (115): *Centaurea dealbata*; *Erigeron speciosus*; *Prunus tenella*	*Androsace sarmentosa** et *A. sempervivoides**, *Anemone sylvestris*, *Anthemis tinctoria*, *Antirrhinum majus**, *Atriplex hortensis**, *Campanula glomerata*, ***Canna indica***, *Commelina communis#*, *Consolida ajacis#*, ***Coreopsis grandiflora* et *C. lanceolata***, ***Delphinium ×cultorum***, *Eupatorium cannabinum*, *Euphorbia marginata**, ***Euryops* spp.**, ***Festuca gautieri***, *Festuca glauca*, ***Gaura lindheimeri* et hybr.**, ***Geranium dalmaticum* et *G. ×cantabrigiense***, ***Glebionis coronaria***, *Humulus lupulus*, ***Chasmanthium latifolium***, *Inula ensifolia*, *Ipomoea purpurea**, *Iris pumila*, *Linum austriacum*, *Lunaria annua#*, *Malva sylvestris*, *Nicandra physalodes**, *Oenothera missouriensis**, ***Opuntia* spp.**, *Portulaca grandiflora** et hybr., *Prunus tenella*, ***Pseudolysimachion incanum***, *Rudbeckia laciniata#*, *Ruta graveolens#*, ***Santolina chamaecyparissus***, ***Satureja hortensis***, *Sedum sarmentosum#*, ***Sempervivum arachnoideum***, ***Silene schafta***, *Stipa tenuissima*, ***Streptocarpus saxorum***, ***Tanacetum densum* et *T. haradjanii***, *Teucrium chamaedrys*, *Typha minima*, *Veronica austriaca* et *V. caespitosa* et *V. prostrata*, ***Veronica* cf. *armena* et *V. pectinata***

Table 2. Basic environmental variables (mean ± SD) characterising each cluster type. The data were obtained from the Czech Hydrometeorological Institute.

Cluster no., name and no. of cases	Altitude (m a.s.l.)	Annual mean temperature (°C)	Annual precipitation (mm/year)
1. old villas neighbourhoods of towns (N = 14)	358 ± 103	8.4 ± 1.1	724 ± 171
2. upland settlements (N = 11)	612 ± 224	6.8 ± 1.2	901 ± 149
3. modern neighbourhoods (N = 28)	312 ± 114	8.9 ± 0.9	610 ± 115
4. old rustic settlements (N = 26)	395 ± 86	8.3 ± 0.7	683 ± 102
5. modern rustic settlements (N = 40)	318 ± 112	8.7 ± 0.9	633 ± 139
6. unclassified sites (N = 55)	398 ± 181	8.1 ± 4.2	710 ± 508

Three statistical tests were performed to assess the differences between the clusters: proportion of alien taxa and proportion of transient and core taxa. Statistical differences between the clusters were tested using arc-transformed values, ANOVA and multiple comparisons by Tukey's test in R 3.2.1 for Windows (https://cran.r-project.org/bin/windows/base/old/3.2.1). Basic statistics on urban types were performed in STATISTICA 12 (www.statsoft.com) presented in Suppl. material 3.

Results

Assemblages of the ornamental flora

Using the COCKTAIL method, we defined 17 plant assemblages (i.e. species groups) across all sites. Based on the 17 plant species groups, five clusters were defined from the 119 sites using a logical operator, similar to classifying vegetation units. No reasonable pattern was found in the remaining cluster, which includes 55 sites (i.e. 32% of all sampled sites). This cluster was characterised as an unspecific ornamental flora, since no potential subgroup was sufficiently pronounced in its composition, habitat demands and cultural indication.

Clusters derived from lists of diagnostic taxa

The clusters were named according to the prevailing type of settlement: (1) old villas neighbourhoods of towns, (2) upland settlements, (3) modern neighbourhoods, (4) old rustic settlements and (5) modern rustic settlements. The taxa, reported below, represent examples of typical taxa (see Fig. 1 for the distribution of sites attributed to each cluster in the study area).

Cluster 1 – old villas neighbourhoods of towns (N = 14)

This cluster is characterised by (i) woodland understorey taxa, often growing semi-spontaneously in the shadow of trees and includes both native (e.g. *Asarum europaeum*,

Convallaria majalis) and alien species (e.g. *Helleborus* spp., *Matteuccia struthiopteris*); (ii) nutrient-demanding taxa domesticated on stone walls or in rockeries (*Asplenium trichomanes*, *Cymbalaria muralis*, *Pseudofumaria lutea* and *Sedum spurium*); (iii) indoor plants kept in the garden over the summer (*Erica cinerea* and *Euphorbia milii*) and (iv) ornamental shrubs (*Rhododendron* spp. and *Rosa ×centifolia*). These gardens were created around large villas built in wealthy residential areas between ~ 1870–1940. Their common style of an English garden is linked with the dominance of shrubs and trees along with lawns. Later, the need for easy and cheap upkeep of spacious gardens resulted in a selection of long-lived, undemanding and low-maintenance taxa (such as trees), persisting through clonal reproduction (such as shrubs) or even forming stable generative populations. Yet, these gardens harbour the lowest number of aliens amongst all the clusters.

Cluster 2 – upland settlements (N = 11)

This cluster is rich in taxa tolerating cold climates and less fertile soils and demanding higher air moisture (e.g. *Primula denticulata*, *Papaver croceum*, *Begonia* aff. *×tuberhybrida*, *Athyrium filix-femina*). Extensive rockeries, rich in taxa from genera such as *Saxifraga*, *Sedum* and *Sempervivum*, are specific to these sites. Many of these uncompetitive and stress-tolerant taxa are of alpine or boreal origin and their local cultivation is enabled by nutrient poor soils, which are only rarely colonised by fast-growing competitive weeds, such as *Elymus repens* or tall annuals. Many alien taxa found in gardens maintain stable self-sowing or clonal populations (e.g. *Achillea ptarmica*, *Dianthus barbatus*). On the other hand, some taxa, which had been traditionally associated with this cluster (e.g. *Calystegia pulchra*, *Myrrhis odorata*, *Aconogonon polystachyum*), are infrequently planted in recent times. In dispersed mountain settlements, ruderal and semi-natural habitats bordering on gardens, these especially often comprise resistant and hardy herbs such as *Helianthus ×laetiflorus*, *Hemerocallis* spp. or taxa invading surrounding natural vegetation, such as *Digitalis purpurea*, *Lupinus polyphyllus* and *Telekia speciosa*.

Cluster 3 – modern neighbourhoods (N = 28)

This cluster includes many woody taxa which constitute ~70% of the local diagnostic taxa. Shrubs and trees are popular owing to their representative appearance and low maintenance. They include taxa with evergreen leaves (e.g. *Pyracantha coccinea* and many conifers), cultivars with columnar (*Populus nigra*) or tortuose habitus (*Corylus avellana*, *Salix matsudana*), coloured branches (*Cornus alba*) and variegated (*Salix integra* cv. Haruko-Nishiki) or dark leaves (*Prunus cerasifera* cv. *Pisardii*). Lianas (*Aristolochia macrophylla*, *Campsis radicans*, *Wistaria sinensis*), tall grasses (*Bambusoideae* family, *Cortaderia* spp., *Pennisetum* spp.) and virgate low shrubs and semi-shrubs (*Caryopteris ×clandonensis*, *Cotoneaster* spp., *Jasminum nudiflorum*, *Perovskia* spp.) are also very popular. On the contra-

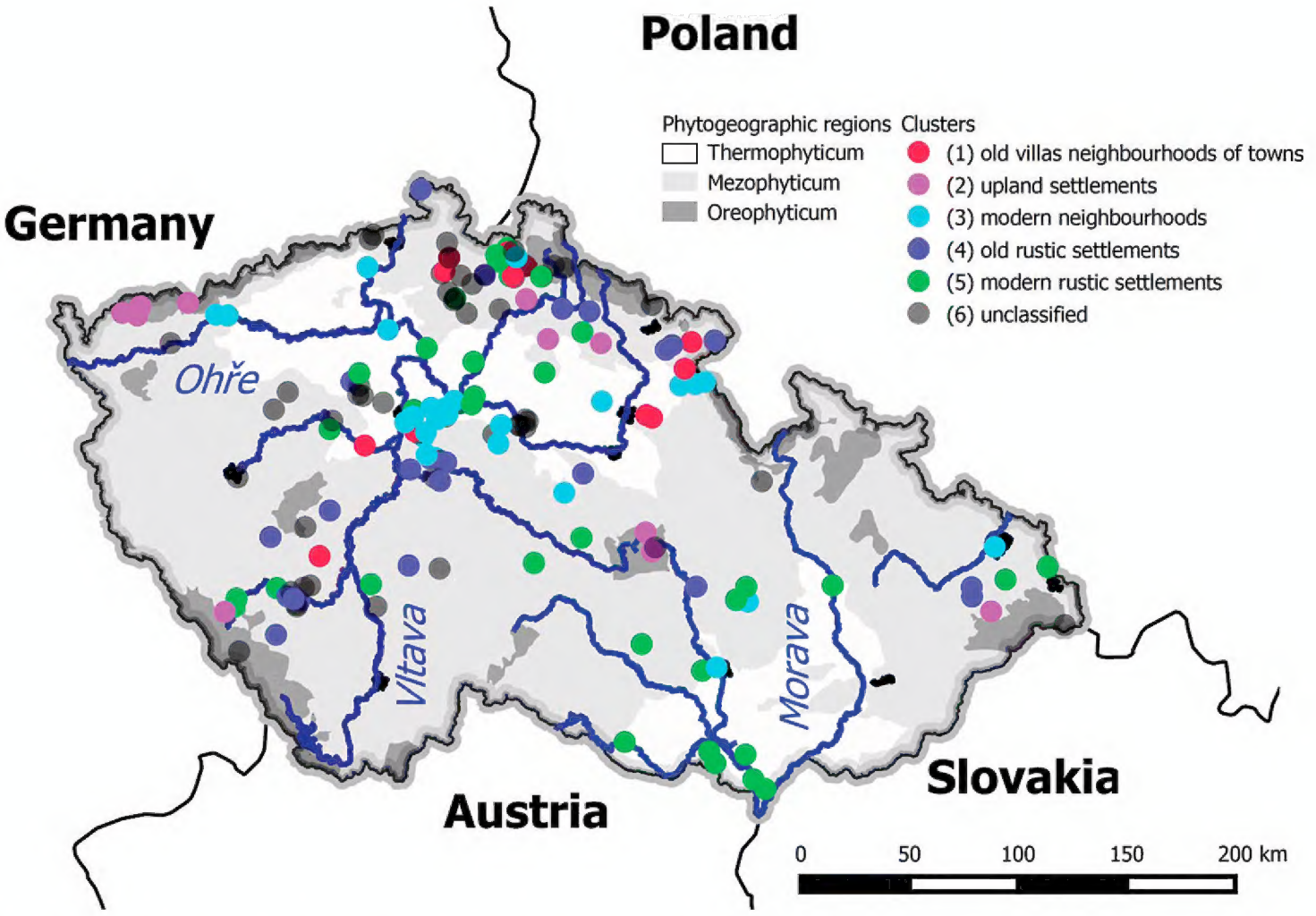

Figure 1. Map of sample sites in the Czech Republic. Phytogeographic regions, reflecting the climatic conditions, are indicated by three shades of grey. Thermophyticum includes warm areas with a thermophilous flora and vegetation. Mesophyticum harbours flora and vegetation typical of the central European temperate zone. Oreophyticum is a cold region with mountain flora and vegetation corresponding to forests of the boreal zone, with smaller areas above the timberline similar to habitats in the arctic zone (see Kaplan 2012).

ry, ornamental annuals, dependent on sowing and weeding, are entirely absent amongst the diagnostic taxa of this cluster. Gardens are typical of modern detached houses.

Cluster 4 – old rustic settlements (N = 26)

Joint cultivation of ornamental and utility plants in hoed beds characterise this cluster. Crops such as *Levisticum officinale* and *Rheum rhabarbarum* partly hold an ornamental function. *Anethum graveolens* is often combined with roses to grow under their protection. Some native taxa (e.g. *Agrimonia eupatoria*, *Rosa canina* and *Sambucus nigra*) often establish spontaneously and are tolerated both for ornamental and practical purposes. Hoeing, sowing and weeding are suitable management practices for cultivation of annuals (i.e. *Cosmos bipinnatus*, *Nigella damascena* or *Tagetes* spp.) or geophytes which are easily replanted (e.g. *Aconitum napellus*). Carnations (*Dianthus* spp.) along the edges of garden beds are another widely shared tradition. Amongst trees, taxa planted for fruits entirely prevail over ornamental trees. Low numbers of ornamental taxa and their arrays follow local tradition since the 19th century (e.g. *Polemonium caeruleum*, *Alcea*

rosea and *Phlox paniculata*). However, cultivation of, for example, *Syringa ×chinensis* and *Vaccinium corymbosum* is of modern origin.

Cluster 5 – modern rustic settlements (N = 40)

This cluster shares many taxa with cluster 3, but it has its own group of diagnostic taxa, such as (i) lianas (*Humulus lupulus*, *Ipomoea purpurea*), covering garden fences; (ii) taxa of rockeries, often robust and drought-resistant chamaephytes (genera *Iberis*, *Opuntia*, *Oenothera missouriensis*, *Ruta graveolens*, many taxa from the Lamiaceae family); (iii) self-spreading native taxa of dry grasslands (*Iris pumila*, *Anemone sylvestris*, *Linum austriacum*, *Prunus tenella*); (iv) annual self-sowing alien taxa (*Euphorbia marginata*, *Portulaca grandiflora*, *Commelina communis*, *Consolida ajacis*); and (v) tall nutrient-demanding perennials (*Canna indica*, *Rudbeckia laciniata*). These gardens usually border recently-built family houses.

Alien, core and transient taxa

The clusters significantly differed in the proportion of alien taxa, ranging from 73% (upland settlements) to 93% (unclassified cluster; Fig. 2). The highest number of aliens occurred in modern neighbourhoods and in old rustic settlements (Fig. 2). The multiple comparisons analysis revealed that the old villas neighbourhoods of towns comprise fewer aliens compared to other sites. There were no significant differences amongst the other groups.

The proportion of the transient taxa was not statistically different amongst the individual clusters. The lowest mean proportion of transient taxa was 29.7%. In addition, the clusters differed in the proportion of alien core (persistent) taxa (Fig. 3), with the highest proportion in the unclassified cluster (22.5%) and the lowest (7.1%) in modern neighbourhoods. The analysis showed a generally low number of taxa amongst the core aliens, indicating a higher probability of new introductions in the future.

Discussion

Classification of the ornamental flora

We based the categorisation of the ornamental flora on our field experience and used a formalised statistical approach to demonstrate that our assumptions about the assemblages of garden plant species can be expressed in a way that is usually applied to vegetation studies (see statistical forming of sociological species groups by Chytrý 2009 or Chytrý 2012 for a review). The COCKTAIL method allows for the transferability of species groups across scales, by combining grid-based distribution and vegetation data (Petřík and Bruelheide 2006). Although the method was not originally designed

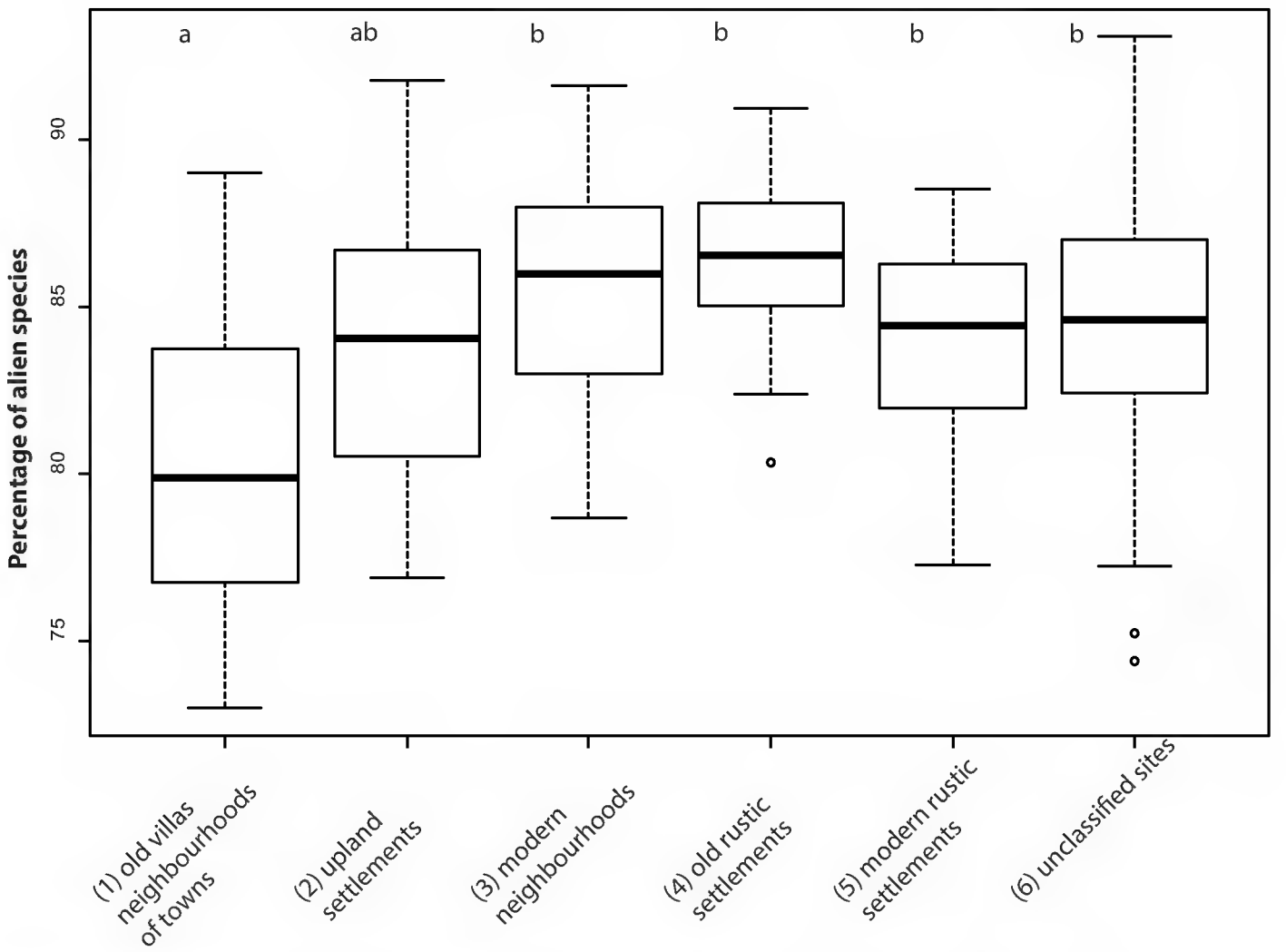

Figure 2. Differences in the percentages (i.e. median, 25th and 75th percentile and min/max values) of aliens amongst all ornamental taxa within clusters of the classified settlement types and within the unclassified cluster. Same letters above the boxes indicate insignificant differences between clusters (ANOVA $F = 5.35$, df (5, 168), $p < 0.001$).

to study natural vegetation, our study is the first to apply COCKTAIL to artificial, non-spontaneous species groups. In most vegetation compendia, human-influenced vegetation is classified based on simple dominance; however, we used the COCKTAIL method to classify the traditionally recognised phytosociological units of various hierarchy (but see Fratarcangeli et al. 2019, who applied the concept of fidelity in the same way as in our study, but on spontaneous vegetation).

Cubino et al. (2014) and Kendal et al. (2012a) compared cultivated floras across urban and rural settlements and found that social factors (i.e. human behaviour) are more important than climate and environmental conditions in determining the distributions of floras. While both studies explored the diversity of ornamental floras in relation to socioeconomic aspects, only Cubino et al. (2016) interpreted plant communities with regard to urban characteristics. These authors found that the differences between the composition of natural vegetation and artificial plant assemblages could be related to permanent residencies of local inhabitants vs. temporal residencies occupied by tourists. In another study by the same authors, Cubino et al. (2017) separated ornamental gardens from irrigated lawns and vegetable gardens. This distinction could not be tested using our dataset, as the structure of our data is totally different from

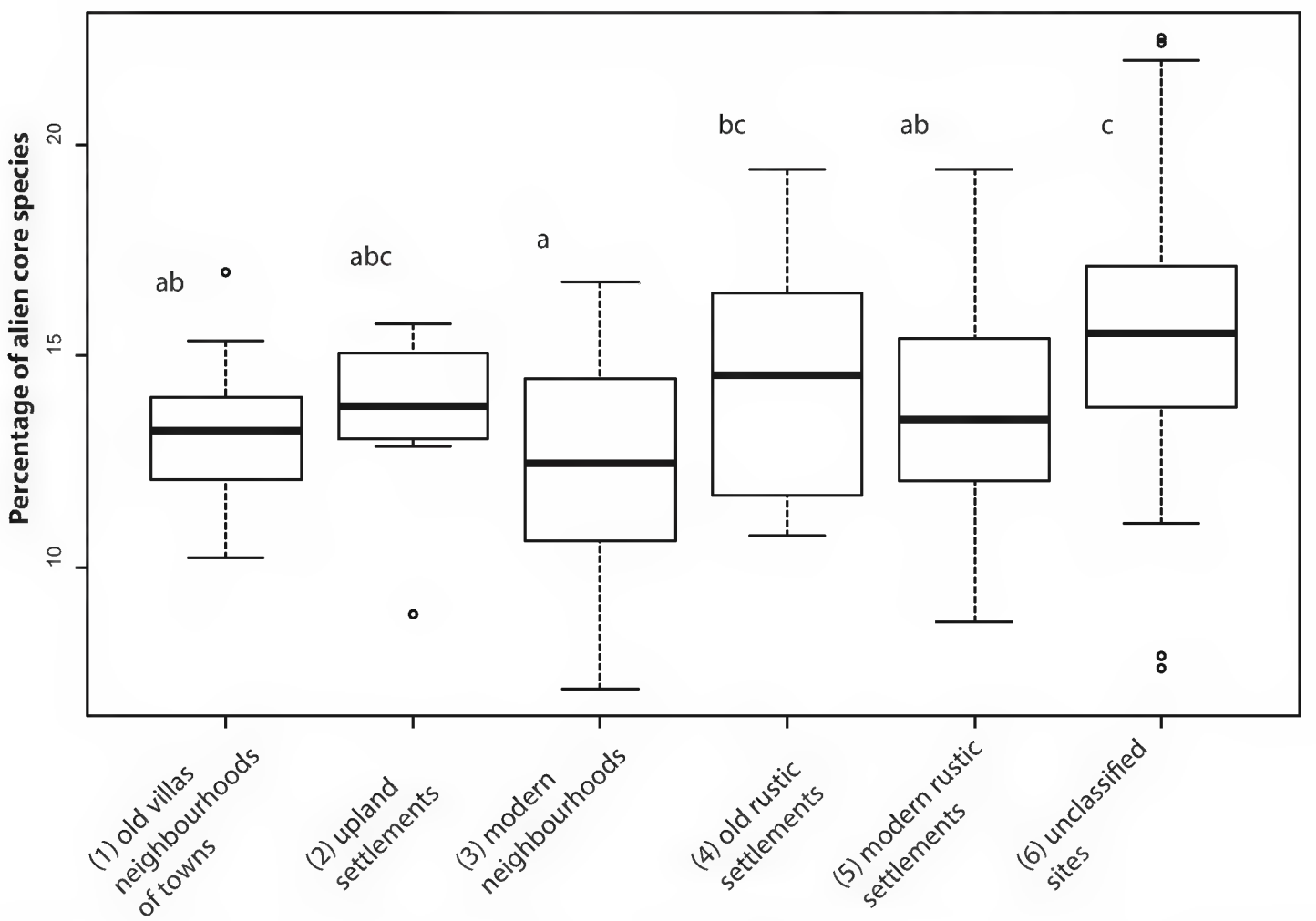

Figure 3. Differences in the percentages (i.e. median, 25th and 75th percentile and min/max values) of core alien ornamental taxa (i.e. frost-resistant cultivated plants that persisted for a long time after abandonment or taxa that occur at many sites) within clusters of classified settlement types and within the unclassified cluster. Same letters above the boxes indicate insignificant differences between clusters (ANOVA $F = 5.69$, df (5, 168), $p < 0.001$).

the coastal ones. In addition, the sampling method and scale (questionnaire and home gardens), used by the cited authors, was sufficient to assess the socioeconomic characteristics which remained unknown to us, as we used data for the urban space only.

The concept of transient and core species, used in the analyses, shows the differences between established species, both naturalised aliens and native, and casual alien species. Both groups represent different levels of risk in the future. The core species have been present for a long time and many of them have the potential to spread after a lag phase; however, the transient taxa represent a larger pool of species waiting for opportunities to invade (Pergl et al. 2016b, Haeuser et al. 2018, van Kleunen et al. 2018). Additionally, potential time lags by core species may play a significant role after their long time of residence.

Ornamental flora and urban types

The information on the structure of settlements was not collected systematically. Therefore, we cannot provide percentage cover accounted for by individual clusters; however,

such information is clearly visible in the remote sensing images. Preliminary delimitation of individual clusters was therefore based on the structure of recorded sites that were chosen to cover relatively homogenous areas in the villages or in towns and cities. The clusters thus represent the structure of buildings and were mainly defined by expert knowledge.

We interpreted each cluster in terms of urban typology and environmental gradients (see Table 2). Our interpretation was based on the correspondence between the species composition of sites and their environmental, social and economic characteristics (Zerbe et al. 2003). Moreover, we carried out some preliminary analysis on the socioeconomic status of the sites, using the data from the Czech Statistical Office and this confirmed that our groups best describe the urban types that were delimited according to our field experience (see Suppl. material 2).

During our field assessment, we also evaluated some distinctive urban structures (see Suppl. material 2 and Suppl. material 3). Old villas neighbourhoods of towns are dominated by spacious gardens, surrounding wealthy houses (e.g. villas), built by the upper social classes between 1890 and 1930 (see Blažek 1998). These neighbourhoods are situated at different altitudes. Most upland settlements are situated in towns, villages or dispersed farmhouse settlements with a harsher climate (see Table 2). Upland settlements were mostly established by the former German population, which constituted an important, locally dominant ethnic minority prior to World War II. In the second half of the 20th century, many houses and gardens were renovated and new homes were built. The expansion of modern neighbourhoods dates back to the 1990s and occurred mainly in peri-urban lowlands with a mild climate. These neighbourhoods form a distinct urban type with a very specific composition of ornamental flora with the highest representations of specialists in gardening (see Suppl. material 2).

A modern style of garden design brought new practices, such as the use of bark chips or gravel (i.e. mulch). The activities of landscape architects and commercial gardening companies brought further radical changes to the local species composition. Old rustic settlements are characterised by cottage gardens in villages or peripheral parts of towns comprising a large number of farmhouses. Traditional rustic architecture is often replaced by modern single-family houses. However, the structure, composition and management of their gardens adheres to traditional habits (e.g. hoed patches, common cultivation of annuals, mixed plantations of ornamentals together with vegetables and a conservative selection of species). Some cemeteries were included because of the presence of folkish ornamental plants. Most sites are situated in lower altitudes. Modern and old rustic settlements share the same tradition of garden designs and gardening methods, except for the use of modern tools. Local fertile soils (often in lowland chernozem areas) and a warm climate allow for the development of species-rich and floriferous front gardens. Their structure is evidenced, for example, by luxuriant combinations of species, ranging from ornamental vines covering walls, unfenced gardens serving a semi-public function to narrow accessorial patches and lining pavements outside garden fences. Local emphasis on the representative role of these gardens is obvious. Most sites are villages or small towns with a significant proportion of new or renovated detached houses with front gardens and public green belts.

During our fieldwork, we identified other potentially important structures, besides the urban and rural structures listed above. Amongst others, these structures include cemeteries, public allotments, cottage colonies and crofts or gardens. We included public spaces such as cemeteries if these grounds were encountered during our urban district surveys. Therefore, these structures were included in all clusters but did not form an individual cluster. It was impossible to distinguish between private gardens and green public spaces in many cases, for example, green spaces in front of private houses. Surprisingly, none of these structures was differentiated as a unique cluster or species group. This may be due to their small size, floristic variability (i.e. cemeteries) or rather unspecific composition (i.e. allotments). However, it could also be that private gardens are over-represented in comparison to other "urban types" such as cemeteries, garden allotments or public parks.

Ornamental flora in various urban types as a source of plant invasions

The observed patterns suggest possible shifts in regional species pools which may correspond to the recent global shifts (van Kleunen et al. 2018). The detailed knowledge of these species pools is crucial for predicting future plant invasions. The invasion potential of species from private gardens differs according to the type of settlement. For example, a typical feature of old park-like gardens in towns (i.e. old villas neighbourhoods of towns) and gardens in upland settlements is the cultivation and successive domestication of ornamentals in semi-natural conditions. Plants in less-maintained parts of gardens or in semi-public spaces have been confronted with natural conditions for a long time, but also supported by episodic weeding or watering. Human assistance seems to be the best approach to promote naturalisation of new aliens (Mack 2000; Pyšek et al. 2011). Many shrubs (e.g. *Symphoricarpus albus* or *Cotoneaster* spp.) and tall herbs (*Rudbeckia laciniata*, *Reynoutria* spp., *Telekia speciosa*) can spread in these habitats for decades and establish invasive populations (e.g. Mandák et al. 2004). Other taxa are rarely cultivated, but form vigorous populations locally (e.g. *Heleborus foetidus*, *Celastrus orbiculatus*, *Cicerbita macrophylla* and *Veronica gentianoides*; see e.g. Červinka and Sádlo 2000). Many taxa spread within rockeries, but only few of these escape to natural rocky habitats (e.g. *Sedum* spp., *Alyssum murale*) or meadows (e.g. *Papaver nudicaule*, *Dianthus barbatus*). Some taxa may pose a threat to the native flora due to genetic erosion of the native taxa (e.g. *Hieracium aurantiacum* in its non-native areas, *Viola cornuta*, *Cerastium tomentosum* and cultivars of *Sedum album*, see Krahulcová et al. 1996) or appear as garden waste (e.g. *Cosmos* spp.).

Gardens in modern neighbourhoods and modern rustic settlements are very rich in taxa which were not present before the 1990s. Many of these escape, especially into novel habitats via interlocking concrete pavements or beds mulched with pebbles. For example, locally escaping populations of *Linaria purpurea*, *Pennisetum alopecuroides*,

Perovskia hybr. and *Thymophylla tenuiloba* have been observed during the surveys. In addition, these habitats also support the escape of some species that were traditionally cultivated but never escaped in the past, such as *Lavandula angustifolia*.

Many escaping aliens are already classified as invasive (Dehnen-Schmutz 2011), some of which are being eradicated or restricted to ornamental plantations, while others are still intentionally planted in the wild, such as *Rhus hirta* or *Symphoricarpos albus* (Pergl et al. 2016b). Our data allow us to comment on the invasion potential of rare taxa with small populations. Their local but copious spontaneous spread indicates that they may become invasive in the future (Dullinger et al. 2017). The high number of ornamental trees and shrubs planted in modern neighbourhoods potentially lead to invasions into the surrounding landscapes (Křivánek et al. 2006; Gregor et al. 2012; Aronson et al. 2015), especially near forests or shrubby vegetation (see e.g. Dobravolskaitė and Gudžinskas 2011). Abandoned private gardens in villas and residences in city centres represent a less serious threat, due to the lack of suitable habitats in the surroundings. Many alien taxa will overcome the climatic barrier in the future, as demonstrated with the ornamental flora of a small German city, where 45 garden-plant taxa are not yet naturalised but likely to become naturalised in the future (Mayer et al. 2017). The ability to naturalise is not directly linked with negative impacts; however, such studies can be used for horizon scanning (Roy et al. 2014) and for the early identification of potentially problematic taxa (Tanner et al. 2017; Roy et al. 2018). Consequently, the frequency of planting in different urban types, combined with the trait analysis of individual species and their ability to escape, can provide direct prioritisation schemes in the future (Kutlvašr et al. 2018).

Conclusions

In this study, we classified human-made assemblages of ornamental taxa. The results show that human-made assemblages of ornamental taxa can be classified using this method, which has been conceived for natural vegetation, formed by basic ecological gradients.

The detected variation of ornamentals mainly follows (i) altitude, associated with climatic or soil gradients and (ii) differences in local traditions, given by the socioeconomic drivers and cultural history. Similar compositional patterns can be expected in other countries, although particular clusters may differ substantially in their delimitation.

In view of the results, new neighbourhoods represent the greatest potential threat for future invasions. These gardens are species-rich, particularly in woody aliens and many of their taxa have been rarely cultivated or even absent until recently. Furthermore, these neighbourhoods are often constructed in peri-urban belts in which the abundance of newly disturbed habitats is suitable for new local escapees and invasions.

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Supplementary material 1

Sampling methods described in Pergl et al. (2016b)

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Data type: species data

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Link: https://doi.org/10.3897/neobiota.52.39260.suppl1

Supplementary material 2

List of characteristics for individual sites: architecture structure and socio-economic and environmental factors

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Data type: measurement

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Supplementary material 3

Box plots for selected six clusters with subjectively recognized urban types

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Data type: statistical data

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